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SECTION V
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SECTION FIVE

PRESIDENTIAL ADDRESS

The Nature of Photosynthetic Products

G. KROTKOV, F.R.S.C.

A fact in itself is nothing. It is valuable only for the idea attached to it, or for the proof which it furnishes.

CLAUDE BERNARD

IT has often been stated that photosynthesis is probably the most important single process on earth. In its course are formed large amounts of organic matter which eventually are transformed into all kinds of organic substances present in plants and animals. Without photosynthesis there would be no life—at least no life as we understand it.

For man, photosynthesis has several values. From the products of photosynthesis he derives not only his food, but also his shelter, his clothing with the exception of the synthetic fibres recently produced, coal and oil as sources of energy, and so on. No wonder that he has been interested in the nature of photosynthetic products and how they are produced by a plant. Considerable work has been done on this subject and it has been concluded that in the course of photosynthesis the plant synthesizes sugars which by subsequent changes give rise to all other organic substances.

The equation for photosynthesis has been assumed to be:

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

The grounds for such a conclusion are as follows: (*1*) During photosynthesis some nitrogen-free substances do accumulate, of which carbohydrates are the most important. (*2*) Accumulation either of sugars or of the products of their condensation, like starch, has been observed in a number of plants. (*3*) The calorific value of the dry matter produced in photosynthesis is almost that of carbohydrates. (*4*). The O_2/CO_2 ratio of the exchange of gas in photosynthesis is very close to 1, as is expected if carbohydrates are produced. (*5*) The absolute amounts of carbohydrates accumulated during photosynthesis have been found to be close to 100 per cent of the theoretical values, on the assumption that CO_2 is transformed into carbohydrates. (*6*) A number of plants can be grown successfully on sugar as their sole source of carbon. Spoehr grew corn heterotrophically from seed to flowering on glucose as the source of carbon.

The belief that during photosynthesis CO_2 is changed first into sugars, and that all other organic substances are derived from these sugars as a result of their subsequent transformations, is held by the majority of people.

Recently, however, the use of isotopes, coupled with chromatography and radioautography, has brought numerous indications that such a belief is too simple. We have sufficient evidence to indicate that CO_2 assimilated during photosynthesis may appear also in products other than sugars.

About fifteen years ago Calvin and his co-workers carried out experiments to observe if plants could absorb CO_2 not only in light but also in darkness, and if the nature of the pre-treatment of the plants affected the magnitude of their subsequent CO_2 fixation. They placed the unicellular alga, *Chlorella*, in darkness for five minutes in the presence of $C^{14}O_2$ and measured the amounts of $C^{14}O_2$ absorbed. Prior to this, they kept *Chlorella* cells for various periods of time either in light or in darkness. The results they obtained are shown in Figure I. Two main conclusions were drawn. First,

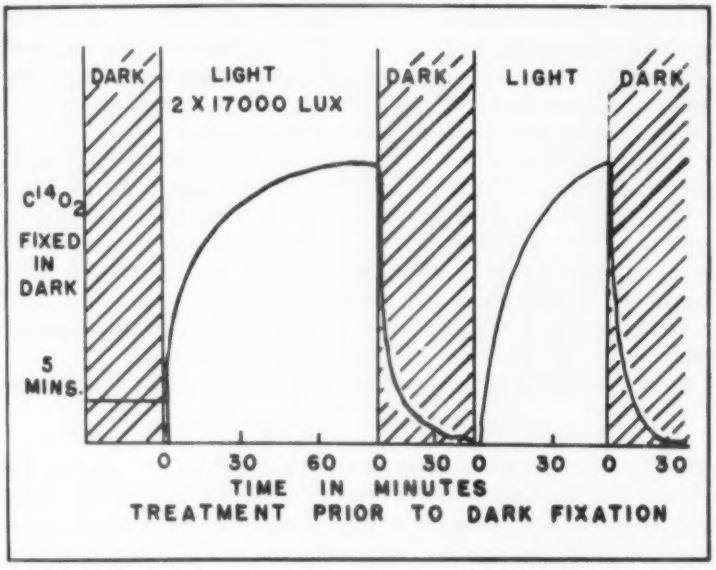

FIGURE 1. Effect of pre-illumination on dark $C^{14}O_2$ fixation by Chlorella (A. A. Benson *et al.* (3)).

Chlorella cells absorb CO_2 even in darkness. Second, the nature of the pre-treatment of *Chlorella* cells does affect the magnitude of their subsequent CO_2 fixation. After a period of dark pre-treatment the amounts of CO_2 absorbed are small; even a short dark pre-treatment rapidly cuts down the magnitude of CO_2 fixation. After pre-illumination the amounts absorbed are much higher. It has been concluded, therefore, that the function of light in photosynthesis is to increase the "reducing power" of green cells, so that the cells are able to assimilate much larger amounts of CO_2. Subsequent research by a number of workers revealed that this "reducing power"

is represented by the accumulation of adenosine triphosphate (ATP) and reduced triphosphopyridine nucleotide (TPNH). The function of increased amounts of ATP and TPNH is to bring about subsequent reduction of absorbed CO_2 to an aldehyde, resulting in the appearance of a triose.

Calvin and his co-workers extracted *Chlorella* cells after photosynthesis in $C^{14}O_2$ and separated various products by chromatography and radioautography. Among the products they found phosphoglyceric acid which is one of the intermediates of the Embden-Meyerhof glycolytic scheme. Since the reactions of this scheme are reversible they suggested that phosphoglyceric acid formed in photosynthesis is first reduced to 3-phosphoglyceraldehyde and then by triose isomerase changed into dihydroxyacetone phosphate. Finally, under the action of aldolase, one molecule of 3-phosphoglycer-aldehyde and one of dihydroxyacetone phosphate condense to form fructose-1, 6-diphosphate. Calvin's scheme for the path of carbon in photosynthesis is shown in Figure 2. As is seen from this figure, for each $C^{14}O_2$ absorbed two molecules of phosphoglyceric acid are formed, one of which is labelled with C^{14}. Following reduction of this mixture of two glyceric acids, and subsequent isomerization of their products to triose, a mixture of labelled and unlabelled phosphoglycer-aldehyde and dihydroxyacetone phosphate is formed. As a result of the chance condensation of these two trioses, the fructose-1, 6-diphosphate formed in photosynthesis initially should be labelled equally in both 3 and 4 positions. Such a labelling has been observed.

If the role of light in photosynthesis is to produce a supply of ATP and TPNH sufficient for the reduction of phosphoglyceric acid to phosphoglycer-aldehyde, it is possible that ATP and TPNH formed in light might also be used to reduce some other substances. It has been reported, for example, that light stimulates the reduction of nitrates. Such information points to the theoretical possibility that some other carboxyl groups, besides that of the phosphoglyceric acid, may also be reduced or that there might be several products of photosynthesis and not just one.

Two definitions of a "photosynthetic product" have been made. According to the broader, or physiological definition, a photosynthetic product is any substance which accumulates during photosynthesis. In sugar cane this is sucrose, in a dicotyledonous plant it may be starch, in brown algae, e.g. *Fucus*, it is mannitol, in diatoms it has been reported to be fat, and so on. According to the more narrow, or biochemical definition, a product of photosynthesis is a substance which is formed directly from the CO_2 assimilated and not as a result of subsequent transformations of the sugars formed initially. With the latter definition of the "photosynthetic product" in mind we may now examine several pieces of evidence for the formation of various organic substances in photosynthesis directly from CO_2 and not by subsequent transformation of sugars.

Our present knowledge of the course and products of photosynthesis has been derived to a very considerable extent from the studies on a uni-

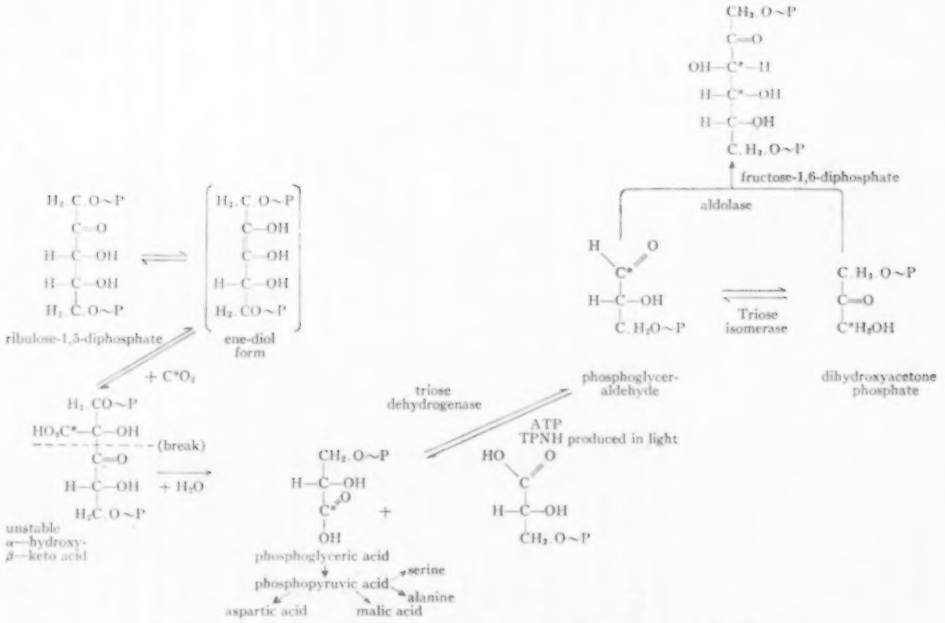

FIGURE 2. The path of carbon in photosynthesis according to Calvin (2).

TABLE I

DISTRIBUTION OF RADIOACTIVITY IN VARIOUS FRACTIONS EXTRACTED FROM DIFFERENT PLANTS AFTER PHOTOSYNTHESIS IN $C^{14}O_2$. AS PER CENT OF TOTAL ACTIVITY ABSORBED. (N.G. DOMAN *et al.* (6).)

		In $C^{14}O_2$ sec.	In $C^{12}O_2$ sec.	Soluble in boiling water	Amino acids	Organic acids	Neutral alcohol soluble (carbohydrate)
Leguminosae	Clover	1	0	100	8.1	1.2	0
	"	1	14	99	8.7	4.1	8.4
	"	1	59	88.8	17.6	10.8	7.3
	"	1	299	57.7	14.2	4.9	16.1
	Bean	1	0	91.8	3.0	6.3	0.2
	"	1	299	54.6	6.5	4.5	17.1
Chenopodiaceae	Sugar beet	2	0	99.2	14.0	29.9	12.5
	" "	2	298	91.6	5.1	2.7	75.5
	Chenopodium	1	0	99.4	16.8	39.4	43.0
	"	1	0	98.5	14.3	30.9	6.6
	"	1	298	96.1	36.2	10.0	23.9
Begoniaceae	Begonia	1	0	100	11.5	57.6	10.1
	"	1	299	73.5	—	—	—
	"	1	299	80.0	6.3	41.3	20.7

cellular green alga, *Chlorella*. A question was raised whether the same photosynthetic products are also formed in plants belonging to other taxonomic groups. To answer this question Doman *et al.* examined photosynthetic products in seventeen species and twelve families of seed plants. Their results for the representatives of three families are given in Table I. From the examination of this table one can see that in every plant almost all the activity derived from the $C^{14}O_2$ absorbed was initially present in substances soluble in boiling water. With the progress of photosynthesis, however, the relative importance of this fraction decreased. In all plants photosynthetic products were represented by sugars, amino acids, and organic acids, but the relative importance of each group of these substances varied from one family to another. Thus after one second of photosynthesis there was only a trace of sugars in leguminous plants, while considerable amounts were already formed in representatives of Chenopodiaceae family. Organic acids were prominent in Chenopodiaceae and especially in Begoniaceae, but they were low in Leguminosae and so on. On the basis of such data it has been concluded that though the same photosynthetic products are formed in various taxonomic groups of plants, their relative amounts may be different. A similar conclusion was reached by Calvin *et al.* (12), who also carried out similar investigations on a number of plants belonging to different taxonomic groups.

Although the O_2/CO_2 ratio of the gas exchange in photosynthesis has been found to be close to 1, it has often been somewhat higher, indicating that at least in some cases other substances, with a lower content of oxygen than carbohydrates, may be formed during illumination. For several reasons proteins have been suggested and a number of experiments have been conducted recently to explore the possibility that they are formed during photosynthesis.

Andreeva and Plyshevskaia placed detached tobacco and corn leaves on a solution of $(N^{15}H_4)_2SO_4$ for twenty-two hours. Thene discs cut from these leaves were placed in glass chambers on moist filter paper and kept there for four to six hours either in darkness or in light, without or with CO_2 (Photosynthesis at the expense of the external CO_2 could take place only in the last variant.) At the end of this time, the leaves were ground and their chloroplastid and cytoplasm fractions were separated by centrifugation. Total protein content and its percentage containing N^{15} were determined for each fraction. The results are shown in Table II.

TABLE II

INCORPORATION OF INORGANIC N^{15} INTO PROTEINS DURING 4–6 HOURS OF INCUBATION. AS PER CENT OF TOTAL PROTEIN N-GEN. (T. F. ANDREEVA AND E. G. PLYSHEVSKAIA (1).)

	Chloroplastids			Cytoplasm		
Experiment	light + CO_2	light − CO_2	dark	light + CO_2	light − CO_2	dark
3	4.64	2.45	0	—	4.65	1.22
4	8.93	4.16	0	14.66	11.25	10.76
5	2.45	1.71	0.48	29.84	23.98	15.41
7	15.41	3.91	2.94	8.07	−0.48	10.20
9	5.87	2.20	2.25	5.87	1.46	5.14
11	3.54	0.85	0.36	1.11	1.42	1.85

Experiments 3–7 with tobacco leaves; 9–11 with corn.

Although considerable synthesis of proteins in cytoplasm did occur in darkness, in chloroplastids this was true only to a much smaller extent. Moreover, in chloroplastids synthesis of proteins was stimulated by light, especially in the presence of CO_2, to a far greater extent than in cytoplasm. These data indicate two kinds of protein synthesis in a plant cell. In cytoplasm proteins are synthesized even in darkness, and light has relatively little effect. In chloroplastids the main protein synthesis occurs during photosynthesis with very little synthesis in darkness.

Synthesis of proteins in chloroplastids during photosynthesis might be due to an increased concentration of sugars which provide the carbon chains for the proteins. To explore this possibility Nichiporovich and his students carried out the following experiments. Detached tobacco leaves were placed for several hours either on $(N^{15}H_4)_2SO_4$ or on a mixture of $(N^{15}H_4)_2SO_4$ and C^{14}-labelled invert sugars. After infiltration, discs cut from such leaves were placed in an atmosphere either of $C^{14}O_2$ or of $C^{12}O_2$ for one to two hours. At the end of this time the proteins extracted from the leaf chloroplastids were analysed for their N^{15} and C^{14} content. The results are presented in Table III.

In leaf discs kept in darkness with $C^{14}O_2$ there was apparently no synthesis of proteins, since the excess atom per cent of their proteins was the same as that initially. Neither was there any incorporation of C^{14} into proteins. However, in light there occurred considerable synthesis of proteins and the carbon for their carbon chains came from the assimilated $C^{14}O_2$.

TABLE III

C^{14} AND N^{15} CONTENT OF PROTEINS EXTRACTED FROM CHLOROPLASTIDS OF TABACCO LEAVES AFTER EXPOSURE EITHER TO $C^{14}O_2$ OR FED C^{14} LABELLED INVERT SUGARS AND $C^{12}O_2$. (A. A. NICHIPOROVICH (11).)

	With $C^{14}O_2$		Leaves fed C^{14} labelled sugars and $C^{12}O_2$			
	Expt. 1		Expt. 2		Expt. 3	
	C^{14} c/m/mg	N^{15} excess atom per cent	C^{14} c/m/mg	N^{15} excess atom per cent	C^{14} c/m/mg	N^{15} excess atom per cent
Initial	0	0.1292	60	0.1140	16	0.0874
Exposed in darkness	0	0.1292	63	0.1026	14	0.0950
Exposed in light	414	0.4940	60	0.1862	14	0.2546

In the leaf discs infiltrated with $(N^{15}H_4)_2SO_4$ and C^{14}-labelled sugars, but kept in $C^{12}O_2$, synthesis of proteins was also stimulated on illumination. However, there was no simultaneous increase in the C^{14} content of proteins, indicating that their carbon chains were not built from the available C^{14}-labelled sugars. One can conclude, therefore, that in this case the carbon chains of proteins came directly from assimilated CO_2 and not from sugars. In other words, CO_2 was assimilated into proteins not *via* sugars, but either from a common precursor or from an entirely different product of carboxylation.

Whether quantitative distribution of various photosynthetic products in a leaf may be affected by external conditions is another question. The first factor to be investigated from this point of view was light. There are two aspects of light: intensity and wave-length. In order to explore the effect of light intensity, Mademoiselle Marie-Louise Champigny exposed detached *Bryophyllum* leaves to $C^{14}O_2$ for six minutes either in darkness or in light of increasing light intensity. At the end of the exposure leaves were extracted and the distribution of C^{14} among various fractions was determined. The results are given in Table IV. Some CO_2 was absorbed in darkness, but

TABLE IV

DISTRIBUTION OF RADIOACTIVITY IN VARIOUS FRACTIONS OF BRYOPHYLLUM LEAVES KEPT IN THE PRESENCE OF $C^{14}O_2$ FOR 6 MINUTES EITHER IN LIGHT OR DARKNESS. (MARIE-LOUISE CHAMPIGNY (5).)

		Soluble				Insoluble	
		Per cent of soluble activity in					
	Total activity per 1 gr. dry wt. c/m	Organic acids and sugar P	Free sugars	Amino acids	Per cent of the total activity in the leaf	Per cent of insoluble, as proteins	Per cent of the total activity in the leaf
Dark	223,000	95.1	0.6	4.3	97.4	50.0	2.6
Light, 5000 lux	867,000	57.0	19.0	24.0	93.8	7.6	6.2
Light, 20,000 lux	3,880,000	49.0	35.5	15.5	77.0	5.2	23.0

with higher light intensity there was an increase in the amounts of the CO_2 fixed. In darkness the bulk of absorbed CO_2 was in organic acids and the proportion fixed in this fraction decreased with increasing light intensity. The reverse was true of sugars, which with the increasing light intensity were progressively more important as photosynthetic products. At weak light intensity, or at a low rate of photosynthesis, a fair proportion of absorbed CO_2 appeared in amino acids. Either at higher light intensity or in darkness their relative importance declined.

In darkness only a small amount of the absorbed CO_2 was in the insoluble fraction, and the relative importance of this fraction went up with increased illumination. Unexpectedly, 50 per cent of the insoluble fraction produced in darkness was represented by proteins. This suggests that proteins may serve as receptors of CO_2 during its fixation.

The role of proteins as possible recipients of absorbed CO_2 was revealed also in Nesgovorova's experiments. This worker used as experimental material detached leaves of eleven different species of seed plants, which were illuminated in the presence of 3 per cent $C^{14}O_2$, either in strong or in weak light. At the end of the different periods of exposure leaves were extracted and the distribution of C^{14} in various leaf fractions was determined. From the results shown in Figure 3 it is seen that in the early stages of photosynthesis more CO_2 appeared in the protein of a bean leaf than in any other fraction.

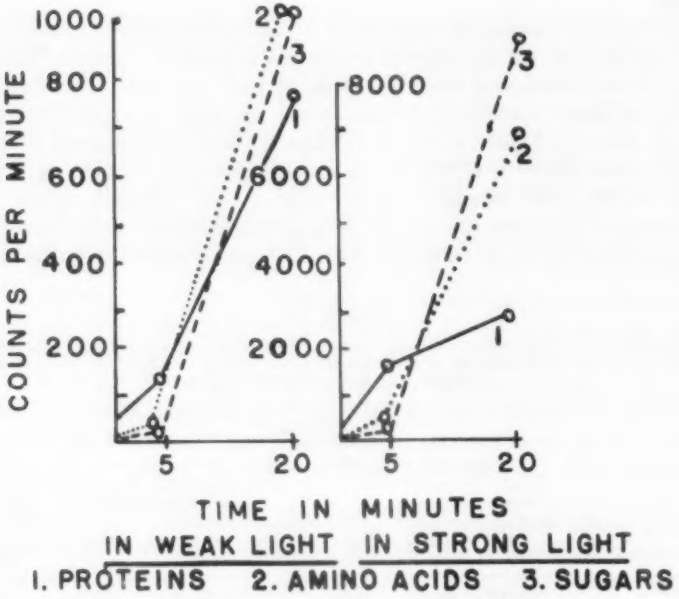

FIGURE 3. Effect of light intensity on the incorporation of $C^{14}O_2$ into different fractions of bean leaves during photosynthesis (L. A. Nesgovorova (10)).

In weak light proteins were important recipients of C^{14} even after twenty minutes of photosynthesis, and in strong light, with time, considerably more activity went into amino acids and especially into sugars. There was a great deal of difference between various species of plants on the relative importance of this fraction during photosynthesis. In some plants, like bean, a great deal of the CO_2 absorbed went into proteins. In other plants, like sugar beet, none of the CO_2 absorbed appeared in proteins.

To investigate the effect of wave-length of light on photosynthesis N. P. Voskresenskaia first infiltrated detached leaves of various plants with KNO_3. The leaves were then illuminated in the presence of CO_2 in either red or blue light having the same number of quanta. At the end of photosynthesis the leaves were analysed; the results are shown in Table V.

TABLE V

ACCUMULATION OF DRY MATTER BY LEAF DISCS AFTER 5 1/2 HOURS OF PHOTOSYNTHESIS IN RED (18,000 ERGS/CM²/SEC) AND BLUE (30,000 ERGS/CM²/SEC) LIGHT. (N. P. VOSKRESENSKAIA (14).)

	Dry wt. added as mg/110 leaf discs		Carbohydrates as per cent of dry wt. added	
	red	blue	red	blue
Corn	37.5	23.8	71.6	63.4
	52.5	14.5	65.6	34.1
Sunflower	32.6	44.9	66.5	37.7
	31.5	9.3	79.3	58.0
	101.0	17.4	42.6	14.4
Bean	38.3	36.0	82.2	46.1

In red light leaves added more dry weight than in blue. Moreover, in red a greater percentage of the added dry weight was represented by carbohydrates than in the blue. One may conclude, therefore, that the wave-length of light has an effect not only on the magnitude of photosynthesis but also on the nature of its products. The results of later experiments by the same investigator, shown in Table VI, indicate that red light favours accumulation of carbohydrates and blue light stimulates accumulation not only of proteins but also of some other non-carbohydrate substances.

TABLE VI

EFFECT OF LIGHT OF DIFFERENT COLOUR ON THE SYNTHESIS OF CARBOHYDRATES AND PROTEINS IN THE PRESENCE OF 1 PER CENT CO_2. (N. P. VOSKRESENSKAIA (15).)

		As per cent of total dry weight added		
		Proteins	Carbohydrates	Proteins + carbohydrates
Corn	red	17	66	83
	blue	21	50	71
	red	33	74	107
	blue	39	25	64
Sunflower	red	22	37	59
	blue	23	24	47

The intensity of the incident light or its wavelength are not the only factors which affect the relative amounts of various photosynthetic products. As is seen in Table VII, under ecological conditions, with the progress of the

TABLE VII

EFFECT OF THE TIME OF DAY WHEN $C^{14}O_2$ WAS ABSORBED ON THE SUBSEQUENT DISTRIBUTION OF ACTIVITY AMONG VARIOUS FRACTIONS. (L. H. FILIPPOVA (7).)

	Expt. carried out at	C^{14} absorbed by leaf c/min/dried leaf preparation	Soluble sugars as per cent of $C^{14}O_2$ absorbed
Zygophyllum rosovii	6 A.M.	170	13.5
	9 A.M.	2130	16.5
	7 P.M.	340	30.3
Lidelofia stylosa	6 A.M.	320	30.6
	9 A.M.	2840	83.5
	7 P.M.	690	94.0

day, and therefore with a change in a number of factors, a progressively large precentage of absorbed CO_2 appears in sugars.

Another factor affecting the fate of assimilated CO_2 is the water content of the soil in which plants are grown. Figure 4 gives the distribution of C^{14} in several products of photosynthesis when wheat plants, grown either on high water content of the soil or under conditions of drought, were used as experimental material. In plants grown under high water content, the first observable product of photosynthesis was rapidly transformed to a number of other substances, and, therefore, quickly dropped down to steady low values. Its drop was delayed under the conditions of drought. In plants grown on soil with high water content a great deal of CO_2 went into phosphorated sugars and sucrose, and considerably less went into alanine. The reverse was true under conditions of drought.

From the evidence presented above one can conclude that although sugars may form the main product of photosynthesis, they certainly are not the only one. Proteins and some other substances are also produced. Moreover, at the beginning of illumination or with low rates of photosynthesis, sugars may not even be the most important product, being replaced by other substances. Finally, not only the taxonomic position of a plant, but also external conditions affect the nature of photosynthetic products and the relative amounts of each.

In view of these conclusions one may ask how this diversity of photosynthetic products can be explained. Two explanations may be suggested: first, the possible diversity of the course of photosynthesis from CO_2 to the final products; second, the possible existence of factors which divert the flow of intermediates either in one direction or in another.

The path of carbon in photosynthesis has been proposed by Calvin and a diagram of it was shown in Figure 2. This path has generally been accepted by the majority of workers in this field, though the following piece of evi-

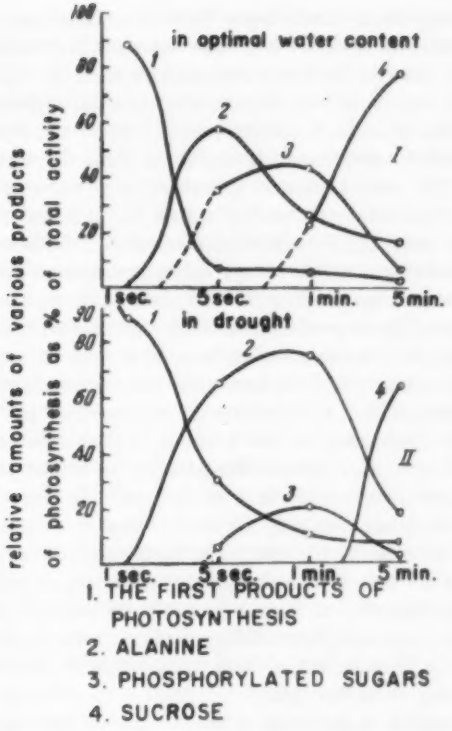

FIGURE 4. Effect of drought on the incorporation of $C^{14}O_2$ into wheat leaves (I. A. Tarchevsky (13)).

dence against it was brought up a long time ago. Since iodoacetate inhibits triose dehydrogenase, an addition of this inhibitor to a photosynthesizing plant ought to suppress formation of phospho-glyceraldehyde and subsequent accumulation of sugars. Early in the formulation of Calvin's theory one of his students (W. Stepka) fed iodoacetate to photosynthesizing tobacco leaves and, contrary to his expectations, he observed continued synthesis of sucrose. Although a suggestion was made at that time that there may be more than one path in the synthesis of sugars from CO_2 this suggestion has not been followed.

According to Calvin's scheme, sugar formed in the early stages of photosynthesis ought to be labelled only in the 3 and 4 positions and the relative amounts of C^{14} in both positions must be the same. A number of workers have confirmed such labelling. Recently, however, Gibbs and Kandler (8) used a better technique for the degradation of sugars which permitted the removal of all six carbons separately one from another. With this technique they

observed that sugars isolated from *Chlorella*, following relatively short periods of photosynthesis in $C^{14}O_2$, were not equally labelled in positions 3 and 4, but that position 4 had more activity than 3. Again these results suggest the existence of at least some deviation from Calvin's scheme.

Within the last year D. C. Mortimer (9) from the National Research Council reported the results of his work on the iodoacetate inhibition of photosynthetic CO_2 assimilation in sugar beet and soybean leaves. He infiltrated leaves with iodoacetate and observed the fate assimilated $C^{14}O_2$. If Calvin's scheme is correct, then inhibition of triose dehydrogenase with iodoacetate ought to bring the following results: cessation of sucrose accumulation, an increase in phosphoglyceric and glyceric acids, and an increase in such substances as alanine, serine, glycine, malic, and aspartic acids. In sugar beet leaves only some of these results were observed. In soybean leaves, although the total amounts of CO_2 fixed were reduced, iodoacetate had almost no effect on the relative distribution of the normal photosynthetic products, which are produced in the absence of this inhibitor. It has been concluded, therefore, that besides the path of carbon in photosynthesis, as proposed by Calvin, there must be a second path. In sugar beet both paths are operative, but in soybean only the second one.

If there are two paths for the CO_2 in photosynthesis then ATP and TPNH may act not only at the phosphoglycerate step of the path, as postulated by Calvin, but also at some other step or steps of the second path. As a consequence, one may have different photosynthetic products, depending on the relative importance of both photosynthetic pathways. And there may even be more than two paths.

The second possible explanation of the diversity of photosynthetic products under the influence of external factors has come from an entirely different field of plant physiology. It has been known for a long time that light affects plants in other ways than through photosynthesis. Plants bend towards light; there may be a diurnal movement of leaves and flowers affected by the intensity of light; in darkness plants grow taller; in some seeds light has a stimulating effect on germination; anthocyanin synthesis in plants is stimulated by light and so on. Since all these changes are brought about by light it is reasonable to expect that there must be some pigment or pigments in plants which absorbs light as the first step in all these changes. Since the action spectrum is the same in a number of these effects it has been concluded that the same pigment is involved.

In December 1959, S. B. Hendricks and his group (4), working at the United States Bureau of the Plant Industry Station in Beltsville, reported isolation of this pigment. They observed that this pigment can be present in two interconvertible forms, depending on whether it was illuminated by red or infra-red light. Since this pigment was present in very small amounts and was thermolabile, they suggested that it forms a part of some enzyme.

The same workers have long been interested in the synthesis of antho-

cyanins in plants. In some of their experiments on this subject they used apples as experimental material and followed out formation of red colour in their skins. Several groups of apples were kept in light of different wavelengths and for control some were kept in darkness. One of the workers by chance bent over the apples kept in darkness and noticed an odour. No such odour emanted from the illuminated apples. Further examination revealed that this odour was caused by ethanol. Hence, apples kept in darkness produced ethanol, while those kept in light did not.

If pigment involved in the synthesis of anthocyanins in apples can be present in two interconvertible different forms, depending on the wavelength of illuminating light, then its action may be different depending on the form in which it is present. If it constitutes a part of an enzymic system, then even a small amount of it may bring about substantial changes in subsequent metabolism. It has been suggested that the operation of such a light-sensitive enzyme could be compared to a double switch. In darkness the switch is open towards ethanol formation and a large proportion of the Embden-Meyherhof scheme intermediates flows in this direction. In light the switch towards ethanol formation is closed and the metabolites are flowing in some other direction. Is it possible that this is the explanation for the accumulation of different photosynthetic products under the effect of red or blue light?

We have seen then that there is considerable evidence indicating that although carbohydrates may form quantitatively the most important product of photosynthesis they are not the only ones, and that the relative importance of various components in a mixture of photosynthetic products is affected by the taxonomic position of the plant, as well as by the external conditions prior to and during the photosynthesis itself. The variety of photosynthetic products may be accounted for by the fact that even in the same plant there may be more than one path leading from CO_2. Since, in various plants the paths may be different, they lead, therefore, to the appearance of different products. Hence, the presence of a special enzyme with a pigment as its prosthetic group, which can be reversed by different light wave-length into one form or another, may direct the flow of metabolites either in one direction or in the other. As a consequence, even the same initial products of CO_2 fixation may lead subsequently to different photosynthetic products.

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